

A NEW SPECIES OF *UNIPORODRILUS*
(OLIGOCHAETA: TUBIFICIDAE) FROM THE GULF OF
MEXICO COAST OF FLORIDA, AND A
PHYLOGENETIC ANALYSIS OF THE GENUS

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Abstract.—*Uniporodrilus purus*, new species, from subtidal sand near Pensacola in northwestern Florida, is described. It is distinguished from all congeners by lacking penial setae. A most parsimonious cladistic hypothesis of the species of *Uniporodrilus* (subfamily Phallodrilinae) is presented. It suggests a basal dichotomy of the genus, with *U. purus* and *U. granulothecus*, both subtidal species, constituting one clade characterized by unpaired male and spermathecal pores, and the four remaining species, all intertidal, representing another clade characterized by a high number of somatic setae and enlarged pharyngeal cavity.

The genus *Uniporodrilus* was established for *Uniporodrilus granulothecus* Erséus, 1979, a subtidal marine tubificid from the east coast of the United States (Erséus 1979). Davis (1985) described a second species assigned to this genus, *Uniporodrilus vestigium*, from Georges Bank off Massachusetts. In a recent revision of the subfamily Phallodrilinae (Erséus 1992a), however, the latter species was transferred to the genus *Atlantidrilus* Erséus, 1982, and at the same time, *Uniporodrilus* was enlarged to include also three taxa previously placed in *Phallodrilus* Pierantoni, 1902: *Phallodrilus scirpiculus* Erséus, 1985 (from Saudi Arabia), *Phallodrilus nasutus* Erséus, 1990(a), and *Phallodrilus bipartitus* Erséus, 1990(a) (both from the Caribbean area). A fifth species recently described from Hong Kong, *Uniporodrilus furcatus* Erséus, 1992(b) is also regarded as a member of this genus, which has been defined by its “varying” penial setae (setae different in size and morphology within bundles) and its granulated spermathecal ducts (Erséus 1992a).

In oligochaete material collected in northwestern Florida by Mr. Jerry McLelland (Gulf Coast Research Laboratory, Ocean

Springs, Mississippi), an additional species of *Uniporodrilus* was discovered. It is described in the present paper, which also includes a cladistic analysis of the species within this genus.

All specimens of *Uniporodrilus purus*, new species, were stained in paracarmine and mounted whole in Canada balsam. The type series is deposited in the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. For comparisons, the whole-mounted specimens in the type material of *U. granulothecus* (also in the USNM) were re-examined.

Cladograms were constructed under the principle of maximum parsimony, using the program PAUP (Phylogenetic Analysis Using Parsimony, version 3.0) by Swofford (1990).

Uniporodrilus Erséus, 1979

Uniporodrilus Erséus, 1979:414–415.—
1992a:22–23.

Uniporodrilus (*partim*): Davis 1985:169.

Phallodrilus Pierantoni (*partim*): Erséus
1990b:54.

Diagnosis (emended after Erséus

1992a) (assumed autapomorphies underlined).—Small marine tubificids. Prostomium distinctly longer than its width at base; generally well set off from peristomium (see Fig. 1). Somatic setae bifid with upper tooth thinner and shorter than lower. [Posterior dorsal setae sharply single-pointed in *U. natusus*.] Penial setae, when present, in fan-shaped bundles or in rings, with bifid or single-pointed, hooked tips. Penial setae absent [in *U. purus*], or from about 6 to about 22 per bundle. Spermathecal pores unpaired, mid-ventral in posterior part of IX [in *U. granulothecus* and *U. purus*], or paired in line with ventral setae in X [in all other species]. Pharyngeal cavity large and much ciliated in some species. Vasa deferentia either entering apical end of, or somewhat subapical on, atria. Atria small, oval, or elongate, curved; when paired, each with two large prostate glands [atrium unpaired in *U. granulothecus* and *U. purus*, with four prostates, at least in *U. granulothecus*]. Atria opening into more or less developed copulatory sacs. Spermathecae [unpaired in *U. granulothecus* and *U. purus*] elongate, with thick-walled, granulated ducts, and small ampullae.

Type species. — *Uniporodrilus granulothecus* Erséus, 1979.

Remarks. — The characteristic shape of the prostomium was referred to as “snout-like” by Erséus (1992a:23). For differences between this diagnosis and the one by Erséus (1992a), see Discussion below.

Uniporodrilus granulothecus Erséus, 1979
Fig. 1A–B

Uniporodrilus granulothecus Erséus, 1979:
415–417, figs. 1–3.—Erséus 1992a:22.

Material re-examined. — The holotype (USNM 56307) and 3 paratypes (USNM 56308, 56309), all whole-mounted.

Remarks. — In the character matrix used for the cladistic analysis of the Phallodriliinae (Erséus 1992a:table I), the prostomium of *U. granulothecus* was coded as “not snout-

like.” This was inferred from the original description (Erséus 1979), which does not include any particular note on the prostomium, except that it is “rounded, about as long as its width at peristomium.” The re-examination of the type specimens, however, showed that the prostomium of this species (Fig. 1A–B) is very similar to that of any congener.

All the re-examined specimens have diatoms in their guts, which suggests that *U. granulothecus* selectively feeds on these algae.

Uniporodrilus purus, new species
Figs. 1C–D, 2

Holotype. — USNM 157046, whole-mounted specimen.

Type locality. — Perdido Key, near Pensacola, Gulf of Mexico coast of Florida; 500 m from shore, about 6 m depth, sand (Oct 1989; J. McLelland).

Paratypes. — USNM 157047–157049, 3 specimens from type locality.

Other material. — Milligan collection: 2 specimens from type locality.

Etymology. — The species epithet *purus* (Latin for ‘simple,’ ‘plain’) refers to the lack of penial setae, and to the single unpaired atria and spermathecae, in this species. All congeners have penial setae, and all but one (*U. granulothecus*) have paired genitalia.

Description. — Fixed worms stout, 1.5–1.9 mm long, 0.16–0.23 mm wide at segment XI; 25–35 segments. Prostomium (Fig. 1C–D) large, clearly longer than its width at base. Clitellum extending over ½X–XII. Setae (Fig. 2A–B) bifid with upper tooth reduced; reduction more pronounced in posterior setae (Fig. 2B) than in anterior ones (Fig. 2A); lower tooth is prolonged in posterior setae (Fig. 2B). Setae 30–45 μm long, about 1–2 μm thick, three per bundle throughout body; but absent ventrally from XI (penial setae absent). Male pore unpaired, mid-ventral, posterior to middle of XI. Spermathecal pore unpaired, mid-ventral, in most posterior part of IX.

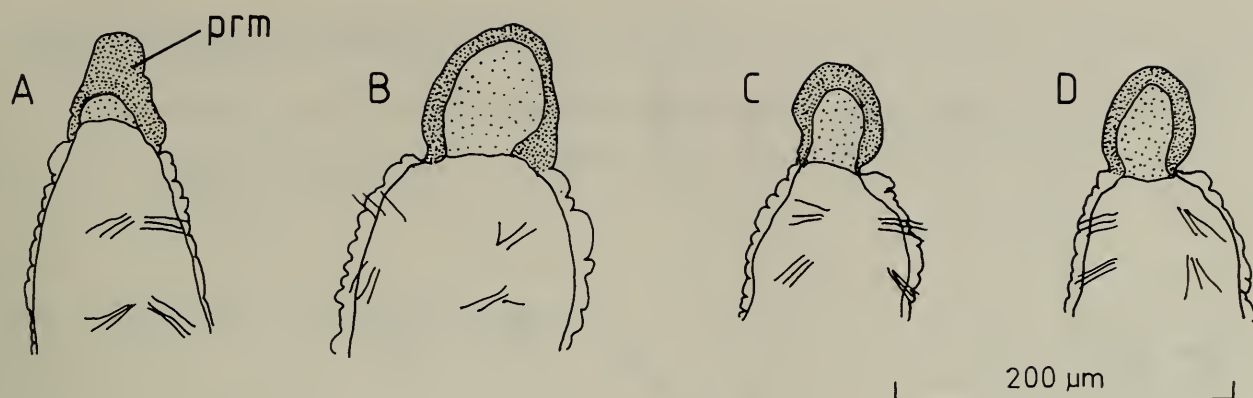


Fig. 1. A–B, *Uniporodrilus granulothecus*, anterior ends of two paratypes (USNM 56308, 56309); C–D, *U. purus*, new species, anterior ends of holotype (C) and one paratype (D). Abbreviation: prm, prostomium. Dense shading indicates epidermal lining, light shading (coelomic?) space within prostomium.

Pharyngeal cavity hollow, but not large. Pharyngeal glands in (III)IV–V. Male genitalia (Fig. 2C) partly paired, partly unpaired. Vasa deferentia paired, much longer than atrium, conspicuously widened (up to 15–22 μm wide) along most parts; cilia few (or absent?), but scattered spermatozoa often present in vasa. Both vasa deferentia entering unpaired atrium somewhat sub-

apically. Atrium oval, 30–40 μm long, 27–30 μm wide, with thin outer muscular lining (1–2 μm thick), and ciliated and somewhat granulated inner epithelium. Atrium opening into unpaired copulatory sac (but details not clear in available material). Lobed bodies of prostate glands located posterio-lateral to atrium (on both sides). They appear broadly attached to atrium, but a division

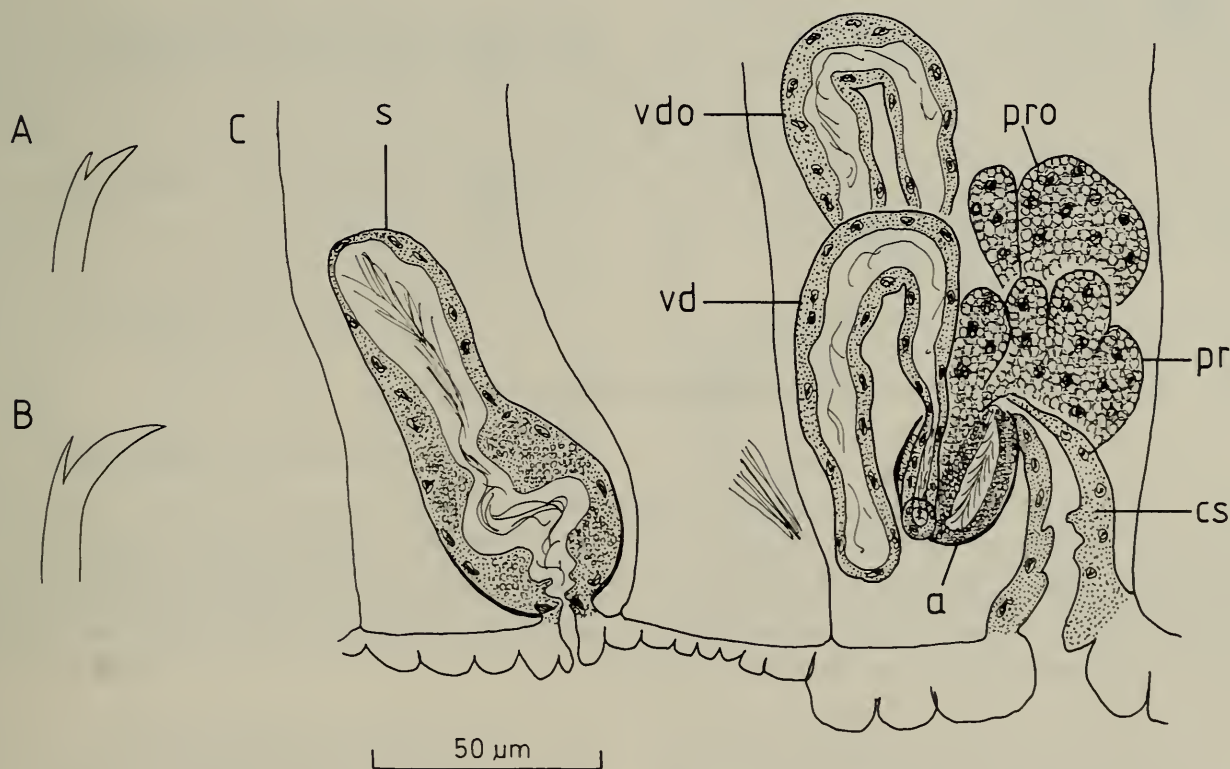


Fig. 2. *Uniporodrilus purus*, new species, A, Free-hand drawing of anterior seta. B, Free-hand drawing of posterior seta. C, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations: a, atrium; cs, copulatory sac; pr, prostate gland; pro, prostate gland of other side of worm; s, spermatheca; vd, vas deferens; vdo, vas deferens of other side of worm.

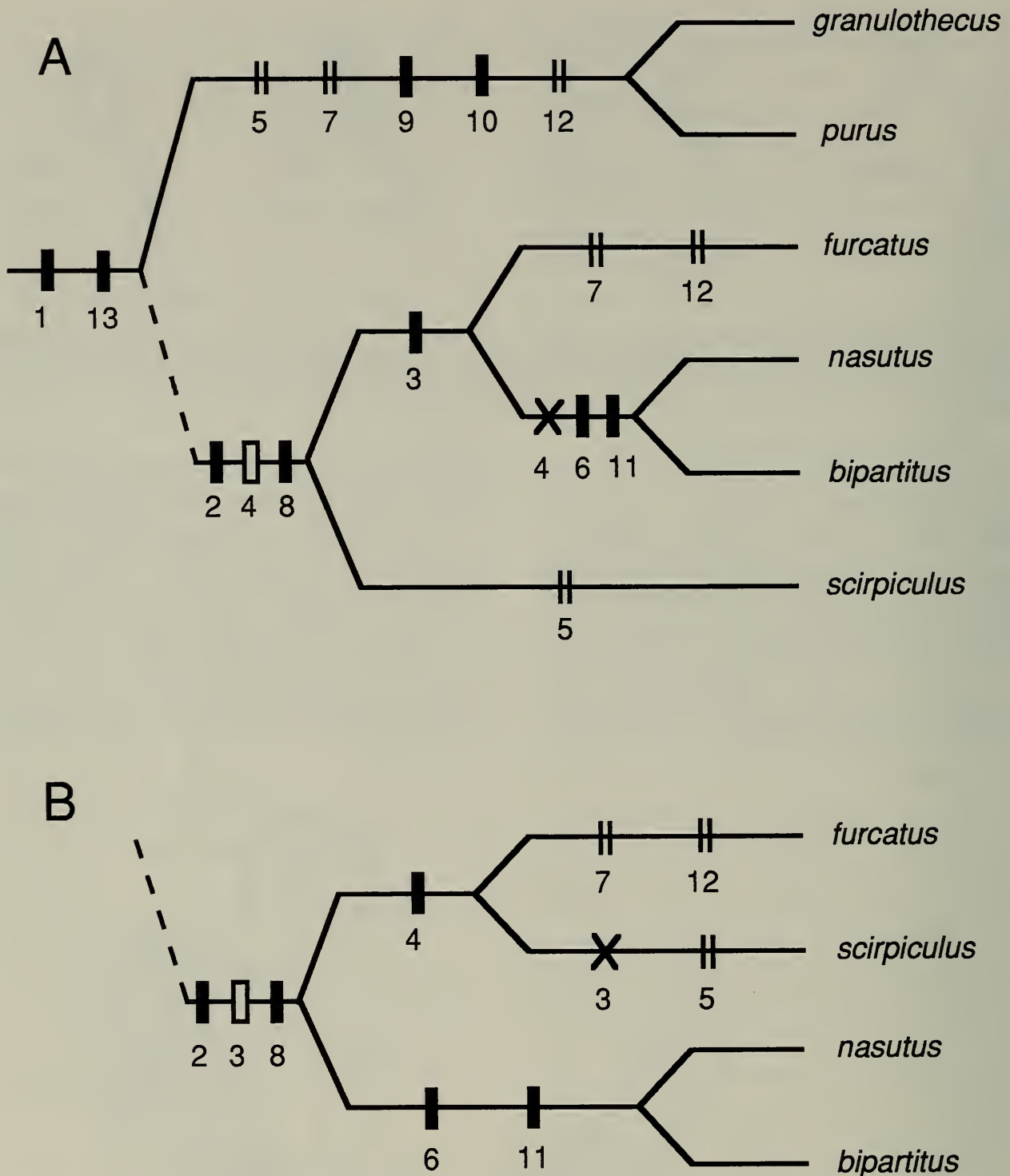


Fig. 3. The two most parsimonious trees (A–B) obtained with the PAUP program for the six ingroup taxa of *Uniporodrilus* (Table 1) and their 13 characters (listed in text, coded in Table 1). Search method: branch-and-bound. Length of trees 17 steps, consistency index 0.765. Rooting at outgroup (*Nootkadriulus*), which is excluded from trees. The clade *granulothecus/purus* is identical in both trees, and therefore only shown in A. The numbers refer to characters. Filled rectangle, autapomorphy; open rectangle, apomorphy that is later followed by reversal; two parallel lines, convergence; cross, reversal.

into anterior and posterior glands (as is normal for Phallodrilinae) not obvious; either anterior or posterior prostates possibly absent. Spermatheca (Fig. 2C:s) unpaired, elongate pear-shaped, 85–100 μm long, maximally 33–45 μm wide. Outer, duct-like

part of spermatheca somewhat granulated, longer and more thick-walled than inner part (ampulla); lumen of duct, however, irregular. Sperm scattered throughout duct as well as ampulla.

Remarks. — This new species is closely re-

Table 1.—Data matrix for parsimony analysis of the species of *Uniporodrilus* (Fig. 3). For characters and character states, see text.

Taxon	Character states, characters 1–13		
Outgroup:			
<i>Nootkadrilus</i> Baker, 1982	00?00	00000	000
Ingroup:			
<i>Uniporodrilus granulothecus</i> Erséus, 1979	10001	01011	011
<i>U. purus</i> , n. sp.	10???	?1011	011
<i>U. furcatus</i> Erséus, 1992b	11110	01100	011
<i>U. scirpiculus</i> Erséus, 1985	11011	00100	001
<i>U. nasutus</i> Erséus, 1990a	11100	10100	101
<i>U. bipartitus</i> Erséus, 1990a	11100	10100	101

lated to *U. granulothecus* (cf. Erséus 1979). Both taxa have somewhat inflated vasa deferentia, as well as unpaired atrium and spermatheca. Moreover, in these two species, the spermathecal pore is in segment IX, not in X as is normal for Tubificidae. *Uniporodrilus purus* is, however, unique within the genus by its lack of penial setae. It is further distinguished from *U. granulothecus* by its stouter atrium, and its less clearly bipartite spermatheca (in *U. granulothecus* the spermathecal duct is much longer than ampulla and has densely granulated walls).

The condition of the prostate glands (with one pair possibly absent) needs to be confirmed when new, preferably sectioned, material becomes available. If any of the prostate glands is absent, this feature is an additional autapomorphy for *U. purus*.

The guts appear empty in all examined specimens. Thus the diet of *U. purus* is unknown (cf. Remarks for *U. granulothecus* above).

Distribution and habitat.—Known only from the type locality in the northeastern part of the Gulf of Mexico. Subtidal sand, at 6 m depth.

Phylogenetic Analysis

Taxa.—The six species of *Uniporodrilus* (Table 1) are the ingroup taxa in the analysis. *Nootkadrilus* Baker, 1982, was selected as the outgroup; according to the cladistic analysis of the whole subfamily Phallo-

linae (Erséus 1992a), this genus possibly is the sister group of *Uniporodrilus*. For the coding of most of the outgroup character states, the descriptions by Baker (1982) were used. For character 9 in the list below, however, material of an unidentified *Nootkadrilus* species and of *N. longisetosus* (Brinkhurst & Baker, 1979) in the senior author's collection was examined.

Characters.—The following characters and character states were used. In the PAUP run, reversals were allowed for all characters.

1. Prostomium not prolonged (0); distinctly longer than its width at base ("snout-like"), and well set off from peristomium (1).
2. Somatic setae maximally three or four (occasionally five) per bundle (0); maximally five to seven (occasionally even eight or nine) per bundle (1).
3. Penial setae all single-pointed (0); at least some penial setae bifid (1).
4. Penial setae of about the same size within bundle (0); some penial setae distinctly larger than others within bundle (1).
5. Within each bundle, penial setae forming a straight row that is parallel to long axis of worm (0); penial setae forming ring within each bundle (1).
6. Penial setae one continuous group within each bundle (0); penial setae in two groups within each bundle (1).
7. Male pores paired (0); unpaired (1).

8. Pharyngeal cavity normal, not enlarged (0); enlarged (1).

9. Pharyngeal glands clearly extending into segment VI (occasionally into VII) (0); not extending further than into V (1).

10. Atria and spermathecae paired, spermathecae in segment X (0); atrium and spermatheca unpaired, spermatheca in IX (1).

11. Atria elongate, not small (0); pear-shaped, small (1).

12. Prostate glands not broadly attached to atria (0); at least one prostate gland broadly attached to atrium/atria (1).

13. Spermathecal ducts not granulated (0); granulated (1).

Results.—The branch-and-bound-algorithm of PAUP 3.0 was used to find the two most parsimonious trees (A and B), which both are shown in Fig. 3. Both trees are fully resolved, with *U. granulothecus* and *U. purus* forming one clade, and the four other species as the sister group of this clade. The topologies of the two trees differ with regard to the branching pattern within the larger sister group: *U. furcatus* is either grouped with *U. nasutus* and *U. bipartitus* (tree A), or with *U. scirpiculus* (tree B). *Uniporodrilus nasutus* and *U. bipartitus* are always together, as they have identical character codings (see Table 1).

However, the character transformations indicated in Fig. 3A–B are not the only most parsimonious optimizations of the present data set. Although not affecting the branching pattern, in tree A, the apomorphic state of character 4 can be interpreted as convergent for *U. furcatus* and *U. scirpiculus*, instead of assuming reversal in the clade *nasutus/bipartitus* (as shown in Fig. 3A). In tree A also, character 5 could be regarded as a basal apomorphy for the whole ingroup, assuming a reversal in the clade *furcatus/nasutus/bipartitus*, or it could be seen as independent autapomorphies for *U. granulothecus* and *U. scirpiculus* (*U. purus* was coded as “?” for this character as it lacks penial setae altogether). In a similar way, in tree B, character 3 could be regarded as con-

vergent apomorphies for *U. furcatus* and the *nasutus/bipartitus* clade. Still, none of these alternative optimizations, or combinations of them, will give other tree topologies than those in Fig. 3.

Discussion

In the previous revision (Erséus 1992a), the varying size and morphology of the penial setae within the bundles, and the granulation of the spermathecal ducts, were assumed to be autapomorphies of *Uniporodrilus*. The “snout-like” prostomium (character 2 in Erséus 1992a:fig. 4) was then interpreted as a synapomorphy of *U. scirpiculus*, *U. nasutus*, *U. bipartitus* and *U. furcatus* (the last-mentioned called “Hong Kong sp. 1” by Erséus 1992a). The present study has shown that *U. granulothecus* as well as the new taxon *U. purus* have prolonged prostomia (Fig. 1) and thus, this feature (character 1 in Fig. 3) can be used to define the genus as a whole.

The character state “penial setae of at least two different kinds within bundle” (character 10 in Erséus 1992a), on the other hand, is treated in a more restricted sense here (character 4 in present paper). In the present analysis, only those two species (*U. furcatus* and *U. scirpiculus*) with distinctly anisomorphic penial setae are coded as apomorphic for this character (character 4 in Fig. 3). The variation of setal morphology in the penial bundles of *U. granulothecus*, *U. nasutus* and *U. bipartitus* is slight, and in *U. purus*, penial setae are absent.

The spermathecal duct is not as long (in relation to the ampulla) in *U. purus* as in the other species, but it is granulated (although not as heavily as in the congeners), and therefore the granulation of the spermathecal ducts (character 13 in Fig. 3) is an apomorphy that still supports the monophyly of *Uniporodrilus*.

The present parsimony analysis suggests a basal dichotomy of *Uniporodrilus*, with *U. granulothecus* and *U. purus* forming the sis-

ter group of the rest of the genus (Fig. 3). Monophyly of the *granulothecus/purus* clade is unequivocally supported by the unpaired male pore (character 7), the restricted extension of the pharyngeal glands (character 9), the unpaired atrium and spermatheca, with the latter in segment IX (character 10), and the broad attachment of the anterior prostates (character 12); characters 7 and 12, however, also (convergently) apomorphic in *U. furcatus*. Depending on which character optimization one prefers, one may also use the ring-shaped penial bundles (character 5) to define this group, based on the assumption that the penial setae were forming rings in the most recent ancestor of *U. granulothecus* and *U. purus*, but not in the common ancestor of the whole genus (see Remarks for the Phylogenetic analysis above). Moreover, both *U. granulothecus* and *U. purus* have distinctly widened parts of the vasa deferentia. This feature appears synapomorphic, but it is not conclusive whether it is unique to these two species, as the vasa deferentia have not been visible in their full lengths in the other members of the genus.

Monophyly of the four other species is supported by the high number of somatic setae (character 2 in Fig. 3) and the enlarged pharyngeal cavity (character 8). Further, two characters suggest that *U. nasutus* and *U. bipartitus* are closely related, the disjunct distribution of setae within the penial bundles (character 6), and the small, pear-shaped atria (character 11). With regard to the phylogenetic position of *U. furcatus* and *U. scirpiculus*, the parsimony analysis is less decisive. Depending on which one of characters 3 (the bifid penial setae) or 4 (the distinctly anisomorphic penial setae) is considered as homoplasious, *U. furcatus* may either be regarded as the sister taxon of *U. scirpiculus* (Fig. 3B), or as the sister taxon of the *nasutus/bipartitus* group (Fig. 3A).

Habitat and geographical distribution were not used as "characters" in the parsimony analysis, but the monophyly of *U.*

granulothecus and *U. purus* seems to be supported by their subtidal habitat, as all the other four species, as well as the outgroup (*Nootkadrilus*), are intertidal. Furthermore, the possibility that *U. furcatus* (from Hong Kong) and *U. scirpiculus* (from Saudi Arabia) are endemic to the Indo-West Pacific region appears to favor their monophyletic status, i.e., in accordance with tree B (Fig. 3); the congeners are all from the Northwest Atlantic and *Nootkadrilus* is so far only known from the Northeast Pacific.

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Literature Cited

- Baker, H. R. 1982. Two new phalloporine genera of marine Oligochaeta (Annelida: Tubificidae) from the Pacific Northeast. — *Canadian Journal of Zoology* 60:2487–2500.
- Brinkhurst, R. O., & H. R. Baker. 1979. A review of the marine Tubificidae (Oligochaeta) of North America. — *Canadian Journal of Zoology* 67: 1553–1569.
- Davis, D. 1985. The Oligochaeta of Georges Bank (NW Atlantic), with descriptions of four new species. — *Proceedings of Biological Society of Washington* 98:158–176.
- Erséus, C. 1979. *Uniporodrilus granulothecus* n.g., n.sp., a marine tubificid (Oligochaeta) from eastern United States. — *Transactions of the American Microscopical Society* 98:414–418.
- . 1982. *Atlantidrilus*, a new genus of deep-sea Tubificidae (Oligochaeta). — *Sarsia* 67:43–46.
- . 1985. Annelida of Saudi Arabia. Marine Tubificidae (Oligochaeta) of the Arabian Gulf coast of Saudi Arabia. — *Fauna of Saudi Arabia* 6 (1984):130–154.
- . 1990a. The marine Tubificidae (Oligochaeta) of the barrier reef ecosystems at Carrie Bow Cay, Belize, and other parts of the Caribbean Sea, with descriptions of twenty-seven new species and revision of *Heterodrilus*, *Thalassodrilides*

and *Smithsonidrilus*.—*Zoologica Scripta* 19:243–303.

- . 1990b. The marine Tubificidae and Naididae (Oligochaeta) of Southwestern Australia. Pp. 43–88 in F. E. Wells, D. I. Walker, H. Kirkman, & R. Lethbridge, eds., *Proceedings of the Third International Marine Biological Workshop: the marine flora and fauna of Albany, Western Australia*. Volume 1. Western Australian Museum, Perth, 437 pp.
- . 1992a. A generic revision of the Phallo-dri-*linae* (Oligochaeta, Tubificidae).—*Zoologica Scripta* 21:5–48.
- . 1992b. Hong Kong's marine Oligochaeta: a supplement. Pp. 157–180 in B. Morton, ed., *The marine flora and fauna of Hong Kong and southern China III*. *Proceedings of the Fourth International Marine Biological Workshop: the marine flora and fauna of Hong Kong and Southern China*, Hong Kong, 11–29 April 1989. Volume

1. Hong Kong University Press, Hong Kong, 526 pp.

- Pierantoni, U. 1902. Due nuovi generi di Oligocheti marini rinvenuti nel Golfo di Napoli.—*Bollettino della Società di Naturalisti i Napoli* 16:113–117.
- Swofford, D. L. 1990. PAUP. Phylogenetic Analysis Using Parsimony. Version 3.0. Computer program distributed by the Illinois Natural History Survey, Champaign.

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